On a New Species of the Genus Haplotaxis; with some Remarks on the Genital Ducts in the Oligochæta.

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With Plates 16—18.

Amongst the material collected by Mr. Keith Lucas during his biological survey of the New Zealand lakes I find two small worms belonging to the genus Haplotaxis, of Hoffmeister (= Phreoryctes, auctorum), which differ from the two species already known—H. gordioides, from Europe and America, and H. smithi, from New Zealand—in being provided with only a single pair of ovaries and oviducts. For this new species, therefore, I propose the name Haplotaxis heterogyne. Justification for placing the worms in this genus, hitherto characterised by the possession of two pairs of female organs, will be found below.

The worm is further remarkable and of general morphological interest on account of the very close structural resemblance, I may almost say identity, of the sperm-ducts with the nephridia. This matter also is reserved for discussion till the characters of the new species have been described.

Haplotaxis heterogyne, n. sp.

Of the two individuals one is sexually mature, the other has only the rudiments of the genital organs. The former was

studied at first entire, stained in alum-cochineal, and mounted in Canada balsam; it was then cut into a series of transverse sections. The anterior end of the other was cut longitudinally; a portion from the middle of the body was cut transversely, and other portions of the worm were studied in glycerine.

The prostomium, as usual in this genus, is remarkably long and narrow, but does not exhibit any annulation. The sensory cells form a thick layer over its whole extent. The Segments I and II are short, and the subsequent ones become progressively larger; the body is much dilated in the region occupied by the sexual products (Pl. 16, fig. 1). Each segment is surrounded by a ring of more deeply stained nuclei at about the level of the chætæ, probably a ring of sensory cells; and a lateral line is evident in transverse section.

The chætæ are four in number in each segment (fig. 15). The single dorsal chæta is only about one third to one half the length of the single ventral one, which is very much stouter than the former; both are, however, alike in form —the basal region is straight, the freely projecting portion is curved so as to be sickle shaped with a simple point. In the mid-body the dorsal chæta is about 0·09 mm., the ventral 0·15 mm. in length. The dorsal chætæ are present throughout the worm.

The clitellum covers Segments XI to XIII and part of XIV; it surrounds the body, but is better developed laterally than either ventrally or dorsally, indeed, it appears in transverse section as thinner dorsally than elsewhere.

I was unable to detect any of the genital pores on the entire worm; but from a study of sections I believe that the two pairs of male pores in Segments XI and XII lie just in front of the ventral chætæ. There is a single pair of oviducal pores in Segment XIII; each pore is external to the line of ventral chætæ, and lies below a slightly overhanging projection of the lateral margin of the ventral surface. In the possession of a single pair of female gonads and ducts this species differs from the other two known species, H. gordioides, and H. smithi; hence the specific name hetero-

gyne. The two pairs of spermathecæ open at the anterior margins of Segments VIII and IX.

Internal Anatomy.

Alimentary System.—The buccal region is noticeably long, extending through the three anterior segments of the body; there is no pharynx, but the buccal tube opens into a gizzard in Segment IV (fig. 1, *g*). This organ is very different structurally from a pharynx, for which it may easily be mistaken unless the worm be studied by means of sections.

It is a cylindrical organ, lined by a thick cuticle (fig. 2); the wall is for the greater part of its extent muscular; the muscle is equally developed on all sides, and consists in the main of a thick circular coat, outside which is a layer of longitudinal fibres, together with others intermingled with the outer lamellæ of the circular coat. A distinct cœlomic epithelium surrounds the whole. From its dorsal and lateral walls a few muscle-slips pass to the body-wall.

In the posterior third of the organ the muscular coat diminishes gradually, and the epithelial cells exhibit more or less numerous goblet-cells, the contained secretion of which is not stained by hæmalum; these goblet-cells open by distinct holes through the cuticle.

Such a structure more nearly resembles a gizzard than a "pharynx;" there is no "dorsal muscular pad," such as occurs in Enchytræids, nor is there any "dorsal ciliated pouch," such as is met with in many earthworms as well as most aquatic Oligochætes. The presence of a gizzard in a so-called "limicoline" member of the order breaks down one more of the barriers which were formerly supposed to separate the aquatic from the terrestrial Oligochætes; and it is remarkable that both Haplotaxis gordioides and H. heterogyne, purely aquatic worms, should possess a gizzard, whilst the majority of aquatic species of terrestrial genera lose the gizzard.[1]

[1] In looking up the literature of the subject, after writing out my notes, I

The œsophagus is quite a narrow tube, lined by ciliated epithelium, which is somewhat folded; it passes backwards, below the sperm-sacs, as far as Segment XII, where it is slightly dilated, and the ventral wall thrown into folds, which are more vascular than elsewhere.

As to the vascular system, the dorsal and ventral vessels are connected by a pair of undulating "commissural vessels" in every segment, as in the other two species of the genus.

Nephridia.—The first nephridium occurs in Segment X, with a funnel in the preceding segment; none are present in the following three segments, in which the genital ducts lie, but in Segment XIV and in each of the subsequent segments there is a pair of excretory organs, and these are larger than those in the tenth segment.

In the immature individual likewise no nephridia are to be seen in the Segments XI, XII, XIII.

In H. gordioides Forbes (4) finds rudimentary nephridia in all the genital segments of a quite immature individual in which no trace of genital organs are yet present.

The disposition and structure of the nephridium is illustrated in figs. 3—8. The nephridial funnel of the post-ovarian organ, at least, has the usual form, with one lip a good deal higher than the other (fig. 9); the canal, after piercing the septum, perforates a row of vesicular cells, which form a loose loop. The cytoplasm of these cells exhibits (when studied under a $\frac{1}{12}$ homogeneous immersion lens) a faint network, but immediately around the canal this network is replaced by more closely granulated protoplasm, which forms a distinct but narrow "wall" to the canal (fig. 8).

These cells do not correspond with the vesicular "peritoneal cells" that surround the nephridium in certain earthworms, or which occur, for instance, in Psammoryctes, as figured by Vejdovsky.

find that Michaelsen (5) has already described this gizzard in H. gordioides in much the same terms as I have above used. In this paper he corrects several errors and misconceptions in the description of the various "species" of Haplotaxis, and shows that the European and American species are identical.

I failed to detect any cilia in the lumen of the nephridial canal.

I have not endeavoured to trace out the course of the lumen in detail, but I note that for the greater part of its course its wall is quite simple, *i. e.* is formed by the faintly granular protoplasm of the perforated cells; but at the apex of the loop there is a differentiation of this protoplasm to form a more distinct, apparently striated, boundary to the lumen (fig. 13, *a*), comparable to the wall of the "ampulla" in the nephridium of Lumbricus.

After leaving the funnel the nephridial loop mounts up alongside the gut, and nearly reaches the dorsal body-wall.

The nephridial canal passes to the body-wall a short distance in front of the ventral chæta (figs. 5, 6, 7), passing amongst the chætal muscles to the chætal gap in the longitudinal muscle of the body-wall. Here the structure of the nephridial cells suddenly changes; the cytoplasm is now very highly granular, the cells, or rather syncytium, becoming much more deeply stained than elsewhere; there is no trace of the cytoplasmic network which is observable in the greater part of the nephridium; the nuclei, too, are rather different (figs. 10, 11). This very granular region may, for convenience, be termed the "duct;" but although I traced the nephridial canal thus far, I was unable to detect any perforation of the more superficial granular cells. They pass through the muscular wall into the epidermis, where they spread out slightly; but I could detect no pore.

This "duct" is readily distinguished from the surrounding epidermis by its affinity for the stain, the epidermal cells appear homogeneous, and spaces exist between the bases of many of the cells. The "duct," however, passes right through the epidermis to the surface.

The nephridium in Segment X appears to be in a state of degeneration; it is relatively smaller than the following ones, and the loop only reaches upward as far as the lateral line, though the diameter of the body is here greater than it is more posteriorly (figs. 12 and 13).

The nephridial funnel, lying in Segment IX, is situated immediately in front of the root of the first testis, as shown in the figure of the longitudinal section of this region of the immature individual (fig. 14). The funnel is smaller than that of the post-ovarian nephridium.

I was unable to trace this first nephridium to the body-wall; it was easy enough to follow it upwards to a point close to the body-wall near the lateral line, some little way in front of the chætæ, but there it seems to cease.

It is interesting to find that Forbes was equally unable to find a pore in the case of the first nephridium in "Phreoryctes emissarius."

Reproductive System.—There are two pairs of testes attached to the anterior wall of Segments X, XI respectively, and on the posterior wall of each of these segments is a pair of spermiducal funnels of a simple plate-like form.

The course of the sperm-duct from funnel to the body-wall is shown in figs. 16—24.

Each of the four sperm-ducts leaves its funnel close to the lower or ventral margin (fig. 32), as described by Beddard (1) for H. smithi; it then passes through the septum, and afterwards behind the funnel and outside the following testis; it soon becomes slightly undulating, and reaches to the level of the lateral line; then, bending down, it reaches the body-wall at a point about midway between the margin of the segment and the ventral chæta (figs. 24, 29).

I have been quite unable, however, to detect any external opening in either of the four ducts, and, indeed, only in the case of the left duct of the anterior pair was I able to trace it actually to the body-wall and into continuity with the epidermis (fig. 29).

Owing to the slight obliquity of the sections and to the displacement due to the previous compression in mounting the specimen, the duct of one side is cut transversely, and that of the other side longitudinally in at any rate part of its course (fig. 28), and in this figure both the upward and downward part of the canal are involved. The duct has almost all the appearance of a nephridium, and its general

disposition in the body is similar to that of the more posteriorly placed excretory organs (cf. figs. 3 and 7 with figs. 16—24). Section across it does not show a definite epithelium, but the lumen appears to traverse a single row of cells. These cells, or rather syncytium, for I cannot detect any boundary to the component cells, are not vacuolated as are the nephridial cells, nor is the protoplasm immediately bounding the lumen of the duct specially granular to form so distinct a "wall" as in the case of the nephridium. Indeed, when first examining the sections I mistook the duct for a nephridium, but a more careful examination of consecutive sections, drawn with a camera, shows quite without any doubt that this tube, if it be a nephridium, at any rate acts as a sperm-duct. In the right duct a group of deeply stained spermatozoa can be seen entering the tube (fig. 32), which, as stated above, starts from the ventral edge of the funnel. In the lumen of the left duct I see a bunch of sperms some distance away from the funnel; these appear both in a portion of the duct cut transversely (figs. 25, 26) and a little further along, appear in a longitudinal section at a bend in the duct (fig. 27), and they can be traced through several consecutive sections. These sperms are deeply stained by the hæmalum, and show up perfectly unmistakably.

In this connection it is interesting to recall the fact that the earlier students of Haplotaxis gordioides believed that the nephridia of these segments acted as sperm-ducts, but Mr. Beddard was the first to identify true genital ducts in the genus in his examination of H. smithi; he describes (1, p. 391) the duct as "a ciliated tube composed of a single layer of columnar cells," and his figure 6 (pl. xxiii) illustrates this statement.

However this may be in H. smithi, the sperm-duct in the present species can scarcely be distinguished structurally from a nephridium, except that the margin of the canal is a little more distinctly marked in the latter, and the cytoplasm of the cells is vacuolated, and the canal is more convoluted than in the sperm-duct, in which, too, cilia can be seen dis-

tinctly in most of the sections. These points of difference require very high magnification, and are not recognisable without a homogeneous immersion lens. But if there is a close similarity between the excretory and genital ducts, there is an immense difference between the spermiducal funnel, with its high ciliated cells forming a conspicuous, broad, thick disc on the septum (fig. 31 et seq.), and the minute nephridial funnel just projecting through a septum.

In the Segments XI, XII I find no nephridia—no tubes, i.e. besides the sperm-ducts,—nor is there any funnel belonging to these tubes other than the flat, wide sperm-funnels. Even in the immature worms no nephridial funnels exist alongside the young sperm-funnels (fig. 37).

It is a curious fact that the sperm-ducts, even in a worm in which ripe sperms fill the sperm-sacs as well as the spermathecæ, and with large ova in their proper segments, should be so difficult to trace; Michaelsen, too, was unable to follow their course in sections of H. gordioides, or to detect the pores, though it is true his specimens do not appear to have been as fully mature as is one of my individuals.

There are two median unpaired sperm-sacs, or, more properly, septal pouches which act as sperm-sacs (figs. 1, 16).

Segment X is filled with loose masses of developing spermatozoa in all stages, mostly fully formed; the Septum X/XI is pushed backwards above the gut, and is also filled with sperms; the end of this sac is at about the level of the end of Segment XI. In Segment XI we have a repetition of this; its hinder wall is also pouched, and reaches to the middle of the thirteenth segment.

There is only a single pair of ovaries, which are situated in Segment XII; I sought in vain for a second pair both in the entire and in sectionised specimens.

A single pair of oviducts corresponding to these ovaries starts from large, wide, flat funnels in Segment XII (cf. figs. 1, 38). The oviduct (figs. 38—42) is a remarkably wide tube, of much greater diameter than the sperm-duct. It is at first directed backwards, and continues in this direction for some

distance; then it curves outwards and downwards towards the latero-ventral angle of the body-wall, which it penetrates well within the Segment XIII, to open just anterior and external to the ventral chæta. The pore is overlapped by a prominent flap, which seems to be entirely due to the greater development of the muscular coats of the body-wall in this segment (fig. 42). The position of this pore so far back in its segment is a very unusual one; for in nearly all the "limicoline" Oligochætes the pore is intersegmental, and even in the earthworms it is usually nearer the margin of the segment than it is in the present worm.

It should be stated that in the younger individual the testes and ovaries are quite small, and except for the rather larger nuclei in the female gonad and a more compact outline of the organ, there is no difference between the two sexes; yet in it the oviduct has already the character described for the adult—a comparatively wide tube (figs. 43, 45) with a wide funnel-shaped opening into the cœlom; the duct is traceable as far as the body-wall, which it reaches near to the ventral chætæ.

There is a striking difference both in dimension and in structure between the oviduct and sperm-duct, for whereas the latter has a very narrow lumen, which appears to be a perforation through a string of cells and is in many respects like a nephridium, the oviduct is quite a wide tube, surrounded by an epithelium of several cells, or, at any rate, a multinuclear syncytium, bearing long cilia within (figs. 44, 46).

The oviducal funnel does not project much into the segment, and in the younger individual has an appearance quite different from that presented by the young sperm-funnels, which are merely smaller representatives of the adult condition. The oviducal funnel, however, is here but little defined (fig. 45); the duct appears in longitudinal section as if the septum were pouched backwards to form a tube, which tube is lined by cells bearing cilia. The lip of the funnel, however, is ill defined; its upper margin is distinct enough and

formed of cubical cells, in which I could not detect cilia, but the lower lip is as yet not prominent; but by the time the worm is sexually mature the lip of the funnel becomes a much more prominent structure.

The hinder wall of Segment XII is pouched, and in the ovisac so formed are some large ova; others lie free in the segment, and still others are free in Segment XIII under the sperm-sac; while in the fourteenth segment still larger eggs distend the body (fig. 1). The presence of eggs in various stages of development in Segment XIII led me to expect a second pair of ovaries here, but I have failed to make them out. It is true that a small group of cells appears in transverse sections to be attached to the underside of the ovisac; this I took at first for a second ovary, but following the sections along, it became evident that it was only a group of small "nutritive" cells adherent to a larger ovum. The mass is free in the segment, and moreover there is no trace of a second pair of oviducts nor their funnels in either of my two specimens.

The funnel of the oviduct (in Segment XII) is so conspicuous an object, its nuclei are so deeply stained, and the funnel is so thick, that I feel sure that I have made no error in this matter. Moreover, in the longitudinal sections the three pairs of young gonads and funnels are quite evident, but no corresponding fourth pair exists.

In Segments XI, XII, and XIII there is a pair of solid glands connected with the epidermis. In the twelfth segment the gland opens in the neighbourhood of the ventral chæta on each side, but in each of the eleventh and thirteenth segments the two glands open below the nerve-cord in the median line. Each gland (fig. 30) consists of a group of long club-shaped cells, with faintly granular and vacuolated contents, which are not stained by hæmalum. The gland projects freely into the cœlom, and the necks of the cells are easily traceable through the epidermis. In each case the gland is nearly of the same length as the segment.

These "copulatory glands" are comparable to the glands of several Enchytræids.[1]

There are two pairs of globular spermathecæ (fig. 1) filled with spermatozoa, communicating with the exterior along the lateral line. They practically fill the anterior half of Segments VIII and IX; there is no differentiated duct, but the epidermis is here invaginated to pass through the muscles and reach the sac. The short tube thus formed is lined by cuticle; there are no special muscles around this tube.

Dimensions.—About 20 mm. by $\frac{1}{3}$ mm; about sixty segments. (The worm was not measured before it was cut in pieces for sectionising, but the portion cut longitudinally measures 10 mm., contains twenty-three segments; and the uncut remains measures 8 mm., contains thirty-one segments; while the transverse series of sections involves two [?] segments.)

Locality.—Lake Wakatipu, South Island, New Zealand, from a depth of 550 feet.

Remarks.

The new worm which I place in the genus Haplotaxis differs from the other two species in a number of minor points, but most noticeably in the possession of a single pair of ovaries and oviducts. The presence of a second pair of these organs has hitherto been a character of the genus which therein differs from all other Oligochætes except the Lumbriculidæ. But apart from the absence of the second pair of female organs, the new worm agrees in all other points with the generic characters as given by Michaelsen in his article in the 'Tierreich,' in the more detailed papers by Beddard, and in his Monograph. The possession of two pairs of sperm-ducts opening independently is another character of the genus, which, however, is shared by Pelodrilus. The latter genus was founded by Beddard (3) for a

[1] Forbes describes a pair of glands, of similar character apparently, in every segment of the body, and suggests that they are sensory.

worm from New Zealand (P. violaceus), in which the sperm-ducts present the peculiarity of both opening independently, but in the same segment. Since this genus is provided with only a single pair of ovaries, I have kept in view the possibility of this being the case in the new worm, but although I did not succeed in tracing the second pair of male ducts to the body-wall, yet there is nothing in the direction of the ducts to indicate that the first pair passes through an entire segment. Moreover, a second species of this genus, P. ignatovi, has recently been described by Dr. Michaelsen (**6**), in which the arrangement of the sperm-ducts is similar to that in Haplotaxis, so that the general arrangement of the genital ducts and pores in this species agrees pretty well with that described in H. heterogyne. But the agreement ceases here, for in all those anatomical characters by which Pelodrilus is distinguished from Haplotaxis the new species now under discussion agrees precisely with the latter. It forms, in fact, with P. ignatovi, a link between the genera Pelodrilus and Haplotaxis as originally characterised. This is seen in the following tabular summary of the characters under discussion, though there are several other differences between the two genera:

	H. gordioides.	H. smithi.	H. heterogyne.	P. ignatovi.	P. violaceus
Chætæ	4 isolated, dors.<vent.	4 couples, dors.>vent.	4 isolated, dors.<vent.	4 isolated, alike	4 couples, alike
Male pores	XI, XII	XI, XII	XI, XII	XI, XII	2 pairs on XII
Female pores	XII/XIII. XIII/XIV	XIII, XIV	XIII	XII/XIII	XII/XIII
Spermathecæ	7, 8, 9	7, 8	8, 9	8, 9	8
Sperm-sacs	Median	Median	Median	Paired; testes free	Paired; testes enclosed
Ovisacs	Median	Median	Median	Median	?

Nephridia and Genital Ducts.

From the point of view of general morphology, this new species of Haplotaxis is of considerable interest owing to the remarkable structural similarity that exists between the sperm-duct and the nephridium. The genus belongs to that section of the Oligochæta which in former days were termed "Limicoline" or Microdrili (mihi), in which excretory segmental organs are in the mature worm absent from the segments containing the genital ducts. This distinction is no longer of so much importance now-a-days, since Vejdovsky (**15**) has shown that in several families, viz. the Chætogastridæ, Naididæ, Enchytræidæ, Tubificidæ, and Lumbriculidæ, these nephridia are present in the genital segments of the immature worm, but disappear by degeneration before the genital ducts make their appearance; and Forbes (**4**) states that in H. emissarius (=H. gordioides) the anterior nephridia in Segments X to XV are small and rudimentary. Now the questions that naturally arise in connection with Haplotaxis heterogyne are: (1) Do nephridia exist in the immature worm in Segments X, XI? If so, then (2) have they disappeared in these segments and been replaced by the sperm-ducts, which have assumed the structure of nephridia? Or, on the other hand (3) have the nephridia persisted in these two segments and been converted functionally into the sperm-ducts? As we have no knowledge of the developmental history of any species of Haplotaxis, we cannot give a direct or certain answer to either of these questions, but the striking similarity between the two categories of organs presented by this species make it scarcely probable that the sperm-ducts have assumed the structure of nephridia, and renders it much more probable that the nephridia have been converted into sperm-ducts, the minute anatomy of which is so absolutely unlike that presented by these organs in other Oligochætes. The small degree of structural difference between the two organs in the present worm may be due to the difference in function. If this third question be answered

in the affirmative; if, that is to say, the nephridia in this worm do act in these two segments as sperm-ducts, then the question as to the homology of these ducts with nephridia in the class is to some degree reopened.[1]

I limit myself to the sperm-ducts, for there is no resemblance between the oviduct and the nephridium, and there need be no debate as to the homology between these. For it does not necessarily follow that if the sperm-duct be shown to be homologous with the nephridium, the oviduct would also be homologous; in point of fact, Vejdovsky (loc. cit., p. 158) expressly states that "there is not a complete homology between the oviducts and the sperm-ducts." And further, it is worthy of note that Bürger (**10**), in a recent paper on the development of Clepsine, finds considerable difference in the mode of development of the male and female organs in the Hirudinea. He shows that in the case of the female organs the entire apparatus, both gonads and ducts, is derived from a V-shaped "anlage"; whereas only the terminal portion of the male duct is derived from a corresponding V-shaped "anlage" in its segment, while the testes, vasa efferentia and v. deferentia develop from quite independent groups of cells, which are not represented in the female system. We may therefore, without prejudice to the larger question, confine ourselves for the moment to the sperm-duct.

It is unnecessary to recapitulate in detail all the points of resemblance and the few points of difference exhibited by the sperm-duct and the nephridium in the Oligochæta in general, or to repeat the historical arguments and views of Claparède and of Lankester in support of the homology; for this has been recently given by Beddard in his account of the development of Octochætus multiporus (**7**). It is sufficient to note that many modern zoologists have withdrawn their adherence to the theory involving any such homology, owing to the facts recorded in recent embryological memoirs; while the whole subject of "nephridium"

[1] See postscript, p. 322.

and "cœlomo-ducts" involved in the more recent theory has been summarised and reviewed by Goodrich (11), and has been accepted, and the ideas of terminology in connection with this view have been extended, by Lankester in his 'Treatise on Zoology' (part ii, p. 32).

According to this modern view, a sharp distinction, founded on the different modes of origin, is drawn between the excretory organs and the genital ducts of the Oligochæta. The former being, according to the observations of Vejdovsky (16) and of Wilson (17), derived from epiblastic ingrowths, the latter from mesoblastic outgrowths from the wall of the cœlom. There is still some doubt, however, as to whether the whole nephridium is epiblastic, for whereas Vejdovsky and Wilson derive it from a "nephric cord" of cells which originate from a superficial teloblast, Bergh (9) insists that the whole organ is developed from the funnel-cell, which he regards as mesoblastic in origin, and not as having pushed its way from the surface into the mesoblast. If this statement of Bergh's should turn out to be true—and it is a case of one good observer against two good observers,—it is clear that a modification will have to be made in the view as to the sharp distinction between the two categories of organs. However this may be, it seems clearly and satisfactorily determined that the genital funnel at any rate is formed as a proliferation of the cœlomic epithelium covering the anterior face of the septum to which the nephridial funnel is attached. Now, Goodrich (12) has shown in a series of valuable memoirs that in the Polychæta the "cœlomic funnel" or "cœlomostome," which functions as a genital funnel, may become grafted on to a nephridium, with or without the loss of the "solenocytes" of the latter organ.

It appears to me that in Haplotaxis heterogyne something of this kind has occurred, for the sperm-funnel is anatomically quite different from the nephridial funnel of the neighbouring segments; while the sperm-duct is pratically indistinguishable from a nephridial tube, and it originates from the funnel at the extreme ventral margin, in the posi-

tion, that is, in which a nephridial funnel, if it were present, would lie; in other words, the duct does not issue from the centre of the funnel as in the sperm-ducts of other Oligochætes. And I suggest that in this worm we have such a composite organ as Goodrich has described in several of the Polychætes (e. g. Goniada, Phyllodocids, Syllids), and to which Lankester gives the name "nephromixium."

In connection with the mode of origin of the sperm-duct from its cœlomostome, it is rather remarkable how little we really know; and it is as well to insist upon this absence of knowledge, and to note precisely how far embryologists have traced (a) the development of the genital funnel, and (b) the development of the duct from this funnel.

Vejdovsky (**15**) has put on record the general course of the history for Chætogaster, and in less detail for certain other genera in which, he says, the same course is followed. The genital funnel appears as a thickening of the peritoneal cells on the anterior face of the septum, and the genital duct grows back from it as a solid cord of cells; this cord reaches the epidermis and becomes hollowed out to form a tube.

In Chætogaster the nephridium has no funnel; but in Stylaria lacustris, which he proceeds to describe (p. 129), he finds that, first of all the nephridium of this segment, VI, gradually undergoes a retrogressive metamorphosis, breaking up into cells, which separate till nothing but the nephridial funnel remains on the anterior face of the Septum V/VI. This, he says, persists for a long time. His next stage figured represents the flat, thick, genital funnel in place of the small nephridial funnel. He does not state in so many words that the latter goes entirely, and it is possible, in the light of Bergh's researches, that it may contribute to the formation of the genital funnel.

At any rate, there is apparently no doubt, in spite of what Roule later on suggests, that a nephridium lies at first in the segment, then disappears; that the genital funnel is formed from the cœlomic epithelium, and gives rise to the genital duct.

Bergh (8), in 1886, describes in detail the development of the funnels in Lumbricus, but he failed to trace the development of the genital ducts therefrom. The genital funnel develops as a thickening of the peritoneal cells immediately above (dorsad of) the nephridial funnel (which of course does not disappear in this earthworm); the development involves partly the cells forming a covering for the back of the nephridial funnel and partly the cells forming the anterior face of the septum itself. The same is true both for ovidnct and sperm-duct, and this very close association of nephridial funnel and cœlomostome is, it seems to me, likely to be of interest when the development of the entire nephridial funnel is fully known.

At present we do not know whether the "marginal" cells of the Lumbricid nephridial funnel are cœlomic in origin. It is quite possible that they are. For the "central cell" is probably the original funnel-cell, which, according to Vejdovsky, divides so as to permit the tubule to communicate with the cœlom. If it should turn out that these peripheral marginal-cells are cœlomic, then the close topographical relation of genital funnel with the nephridial funnel described and figured by Bergh will indicate that the whole "nephridium" of earthworms is a "nephromixium."

A wholly different history is given by Roule (13), in 1889, for an Enchytræid. In the earlier stages in the development of "Enchytræoides marioni" the twelfth segment, in which at a later period the sperm-ducts will arise, contains no excretory organs, though these are present in the preceding segments, IX, X, XI, and in the segments following it, namely, XIII, XIV, etc. The young sperm-duct, when it does ultimately make its appearance, is "en tout semblable à une très jeune néphridie, et deplus, il occupe exactement la place qu'aurait l'organe segmentaire s'il s'était developpé dans la XIIme anneau." Its mode of origin is stated to be quite like that of a nephridium, after this has separated itself from the nephric cord (which is observable in the posterior, but not in the anterior segments); it now consists of

three or four cells more or less fused to form a syncytium; and Roule considers it certain that the sperm-duct is nothing else than the nephridium of this twelfth segment, which is late in appearing, for its special function is not called into play till a much later stage than that of the segmental organ.

It will be noted that this is a very different history from that given by Vejdovsky; and it is well to note that Roule studied sections through successive stages, whereas it appears from Vejdovsky's words that he studied living specimens and entire preparations only.

Then follows Beddard (7), who dealt with a "micronephric" earthworm, Octochætus multiporus, a form in which the earliest segmental organ is a "meganephridium," which becomes broken up into a number of micro-nephridia which are without funnels. According to this author the original funnel of the meganephridium persists in the genital segments, and becomes converted into the genital funnel in each case; whilst the genital duct is for the first part of its course derived from part of the nephridium, which starts to grow once more, and extends back to form the rest of the genital duct (p. 578).

If, now, we consider these various statements, and if we regard, as I believe most zoologists will do, the "Limicoline" Oligochætes as ancestral to the "Terricoline," it seems probable that, phylogenetically, the history of affairs with regard to the organ under discussion has been somewhat as follows:

First stage.—The nephridia act as genital ducts, for Stolc (14) finds that in Aeolosoma spermatozoa may escape from all or any of the segmental organs; in the genital segments these are slightly larger than in other segments, though otherwise similar to them. The funnel of the nephridium is of very simple structure, and there are no representatives of the "marginal cells." Further, according to Roule, the sperm-duct is a late-appearing nephridium in one species of Enchytræid.

Second stage.—A special cœlomostome becomes developed, which, added to the nephridium, increases the efficiency

of the organ as a collector of spermatozoa; we thus have a "nephromixium" comparable to the arrangement in several genera of Polychætes. Such is the condition of the sperm-duct in Haplotaxis heterogyne, as I believe; while in Octochætus multiporus a short part of the genital duct is apparently also purely nephridial in origin.

Third stage.—The cœlomostome gives rise to its own cœlomo-duct, which may either coexist in the genital segment with the nephridium (as in most "terricoline" Oligochætes), or the nephridium, owing perhaps in some cases to the small size of the worm, disappears from the segment during or before the development of the genital duct (as in "limicoline" Oligochætes and Pontrodrilus).

We have, then, to some extent a parallel series of phenomena analogous to those described with so much care by Goodrich in the Polychæta, from which it would appear that the sperm-ducts are not absolutely homologous throughout the Oligochæta.

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B. Remarks on Genital Ducts.

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EXPLANATION OF PLATES 16—18,

Illustrating Dr. W. Blaxland Benham's paper, "On a New Species of the Genus Haplotaxis; with Remarks on the Genital Ducts of the Oligochæta."

Reference Letters.

br. Cerebral ganglion. *b.w.* Body-wall. *c.c.* Cœlomic corpuscles. *c.ep.* Cœlomic epithelium. *c.m.* Circular muscles. *cu.* Cuticle. *d.* Dorsal chæta. *d.v.* Dorsal blood-vessel. *ep.* Epidermis or epithelium. *g.* Gizzard. *gl.* Copulatory gland or its external opening. *int.* Intestine. *l.* Lateral line. *l.m.* Longitudinal muscles of body-wall or other organ. *m.* Muscle-fibres. *m.ch.* Muscles of chæta. *n.* Nucleus. *n.c.* Ventral nerve-cord. *ne.* Nephridium. *ne.d.* Nephridial duct. *ne.o.* Position of nephridiopore. *n.f.* Nephridial funnel. *o.* Ovum. *o.d.* Oviduct. *œ.* Œsophagus. *o.f.* Oviducal funnel. *ov.* Ovary. *ov.s.* Ovisac. *p.* Lateral prominence outside ovipore. *s.* Septum. *s.c.* Circle of sensory cells surrounding a segment. *sp.* Spermatozoa. *sp.d.* Sperm-duct. *sp.f.* Spermiducal funnel. *sp.s.* Sperm-sac. *spth.* Spermatheca or its aperture. *t.* Testis. *v.* Ventral chæta. *v.v.* Ventral blood-vessel. ♂ Male pore. ♀ Female pore.

PLATE 16.

Fig. 1.—View of the anterior extremity of a mature specimen of Haplotaxis heterogyne stained and mounted in Canada balsam. (Camera, × 40.) In the anterior segments the circular segmental series of sensory cells are shown; further back these are indicated in the optical section of the body-wall. The extreme dilatation of Segments XIII and XIV is partly due to compression. The small size of the intestine in the genital segments is shown. *o.d.* is the funnel of the oviduct.

Fig. 2.—A transverse section across the gizzard. (Camera, × 500.) The

greater part of the wall consists of circular muscles, between which, towards the external surface, bundles of longitudinal muscles are intercalated.

Figs. 3—7 represent five sections of one of the post-ovarian nephridia, as seen in transverse sections of the immature individual. These five are selected out of nineteen sections which involve a single nephridium. (Camera, × 120.)

Fig. 3 shows the nephridial funnel projecting through a septum, and a small part of the post-septal region of the nephridium.

Fig. 4 is at about the middle of the series, showing the nephridium at its greatest height.

Fig. 5 involves the muscles of the ventral chæta; the nephridium is passing downwards towards the body-wall.

Fig. 6 is a few sections onwards.

Fig. 7 shows the short "duct," represented by more granular cells (see fig. 10).

Fig. 8.—An enlarged view of a nephridium in such a section as is represented in fig. 4. (Camera, × 500; details as seen with Leitz, $\frac{1}{12}$ homog. imm. lens.) The vacuolated condition of the large nephridial cells, and the distinct "wall" to the canal are seen.

Fig. 9.—A funnel of a post-ovarian nephridium from a longitudinal section, which is neither sagittal nor frontal, but which cuts the worm obliquely. (Camera, × 700.) No details of cell-structure are shown.

Figs. 10, 11.—Two consecutive sections through the "duct" of the nephridium. (Camera, × 700; details under $\frac{1}{12}$ hom. imm.) The cytoplasm of the nephridial cells, or better "syncytium," is no longer vacuolated, but highly granular.

Fig. 10 is a highly magnified view of fig. 7.

Fig. 11 is the next section. It shows the "duct" passing into and through the epidermis, from which it is readily distinguished. I was unable to trace the canal to a pore.

Fig. 12.—A transverse section through the body of the mature individual, nvolving the first nephridium in Segment X. (Camera, × 120.)

Fig. 13.—The same nephridium—next section—more highly magnified. (Camera, × 700.) The cytoplasmic network not indicated. Towards the upper part of the organ the wall of the canal (*a*.) is much thicker than elsewhere.

Fig. 14.—The funnel of the first nephridium, as seen in a longitudinal section of the immature individual. It is smaller than that of the post-ovarian funnel (cf. fig. 9). (Camera, × 700.)

Fig. 15.—A transverse section of the body through the œsophageal region (× 120), showing the relative sizes of the dorsal and ventral chætæ.

PLATE 17.

FIGS. 16—24 represent a series of nearly consecutive transverse sections of the mature specimen through the first pair of sperm-funnels and the second pair of testes. (Camera, × 120.)

In fig. 16 the entire section, with all the organs involved, is drawn; in the rest only the ventral half or less is drawn. In fig. 16 the spermatozoa filling the first sperm-sac and surrounding the gut are shown, but they are omitted in subsequent figures. The worm having been first mounted entire and somewhat compressed, the organs have been slightly displaced, so that the right and left organs are cut through at different planes in a section. On the right side the course of the sperm-duct can be followed easily up to fig. 20, where it has reached its greatest height in the body; it then descends, and the last trace that I was able to detect (fig. 22) was close to the chætal muscles; the base of the chæta is cut through here, but the shaft comes into view and perforates the body-wall nine sections further along. The body-cavity was here filled with a coagulum, which, being stained in hæmalum, rendered it impossible to trace the sperm-duct further; but on the left side the duct was traced right up to the epidermis (fig. 24) (see also fig. 29).

FIGS. 25—27.—Three consecutive sections through part of the left sperm-duct in the region shown in figs. 20, 21, in order to show the structure of the duct and the presence of spermatozoa therein. The sperms (*sp.*) can be traced in several other sections, even when the duct is close to the body-wall (cf. fig. 29). (Camera, $\frac{1}{12}$ hom. imm., Leitz; × oc. 3, Leitz.)

FIG. 28.—A section cutting the sperm-duct (of Segment XII) longitudinally near the upper end of its course, showing the upward and downward limbs of the duct. (Camera, × 700.)

FIG. 29.—From a transverse section (fig. 24), showing the sperm-duct passing through the muscles of the body-wall towards the epidermis, which is reached in the next section (not figured). Spermatozoa are seen in one of the sections across the duct. (Camera, × 700.)

FIG. 30.—The copulatory gland from Segment XIII, as seen in a transverse section of the mature worm. (Camera, × 700; details under $\frac{1}{12}$ hom. imm.)

PLATE 18.

FIGS. 31—36 show the sperm-funnel and the commencement of its duct. Camera, × 700; details under $\frac{1}{12}$ hom. imm.)

FIGS. 31—34 are four consecutive sections through the first sperm-funnel on the right side.

Fig. 31 cuts through the lip of the funnel.

Fig. 32 cuts through the middle of the funnel; it shows the sperm-duct issuing from the extreme ventral margin, and a few spermatozoa, with which the segment is filled, are seen entering the mouth of the duct.

Fig. 33 cuts across the sperm-duct as it bends backwards behind the funnel; a spermatozoa is seen in the duct as a small dot. (This figure is an enlargement of fig. 16.)

Fig. 34, which is from a section between those drawn in figs. 16 and 17, involves the lip of the funnel and the root of the second testis, below which is the sperm-duct.

Fig. 35 is an enlarged view of a section near that represented in fig. 18. The funnel is no longer present; the second testis is seen, and the sperm-duct is cut through below the testes, and again on the right of the figure.

Fig. 36, from a section intervening between those represented in figs. 19 and 20, shows the sperm-duct passing upwards behind the septum. The ciliation of the duct is shown in this figure.

Fig. 37.—A longitudinal section through the second sperm-funnel and duct and the ovary of the immature specimen. (Camera, × 700.)

Figs. 38—42 represent a series of successive but not consecutive transverse sections showing the oviduct. (Camera, × 120.)

In fig. 38 all the organs in the left half of the section are shown; in the remainder only the organ in question. In this section the oviducal funnel is cut through at about its widest part, but somewhat obliquely.

Fig. 39 (which represents the fourth section after the previous one) cuts through the lower part of the funnel, which was torn in the section (cf. fig. 44). In this figure half of the copulatory gland is seen (cf. fig. 30).

Fig. 40 (the fourth section beyond the previous one) cuts the oviduct somewhere about the middle of its course.

Fig. 41 represents the eighth section from the last, shows the duct entering the body-wall, which is here and in the next few sections much thicker than elsewhere.

Fig. 42 is the third from the preceding; the duct is now close to the epidermis. In the following section (not figured) the duct opens to the exterior below the prominence (*p.*), due to the greater development of the longitudinal muscles of the body-wall.

Fig. 43.—The oviduct (in longitudinal section) of the immature specimen. (Camera, × 120.) It shows practically its full length, and it will be noticed that it reaches back as far as the chætal muscles.

Fig. 44.—A transverse section of the oviducal funnel (see fig. 39), the wall of which has been ruptured during manipulation. (Camera, × 700; details under the $\frac{1}{12}$ hom. imm.)

Fig. 45.—Enlarged view of fig. 43, combined from it and neighbouring

section. The lip of the funnel is only definitely formed on its dorsal border, where it is seen passing upwards in front of the septum; on this lip I could detect no cilia, though these are quite evident in the duct itself. The septum is seen to be somewhat pouched backwards. (Camera, × 700.)

Fig. 46.—A transverse section of the oviduct about mid-way between figs. 40 and 41. (Camera, × 700.)

Postscript.—Since despatching my MS. from New Zealand I have come across an article by Mr. Beddard in the 'Proc. Zool. Soc.' in 1902, vol. ii, p. 89, which I had unfortunately overlooked. In discussing the female reproductive organs of Eudrilus he introduces some remarks, on p. 95, relative to "nephridia" and "cœlomo-ducts" which are in agreement with the views put forward in the present paper. He is "not convinced" that the oviducts and sperm-ducts are "cœlomo-ducts." Further, he makes use of Bergh's account of the origin of the genital duct from the "peritoneal" covering of the nephridial funnel in the same manner as I have done, and indicates the probability of part of the nephridial funnel being peritoneal in origin. He concludes (p. 97), "It appears to me that these various considerations show that it is at least premature to regard the gonad-funnel of the Oligochæta as essentially different from the nephridial funnels."

I regret that by this oversight my friend's views receive no recognition in the body of my paper.

June 6th, 1903.